

***Nipponnemertes fernaldi*, a new species of swimming monostiliferous hoplomertean from the San Juan Archipelago, Washington, U.S.A.**

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*Abstract.*—*Nipponnemertes fernaldi*, new species, is described as a member of the order Hoplonemertea, suborder Monostilifera. In general morphology, it appears to be most closely related to the genus *Nipponnemertes* (family Cra-tenemertidae) and the new species is placed in this genus. The significant characters are explained and discussed.

Among numerous nemerteans collected in the San Juan Archipelago, Washington in 1964 were specimens of a monostiliferous hoplomertean here described as new. This nemertean possesses characters that exclude it from any of the previously described species of *Nipponnemertes*. New information on the morphology of monostiliferans is provided with respect to: the central stylet-basis complex of the proboscis; the cerebral organs (with a sensory canal and a sac-like canal); a pair of middorsal epidermal folds in the anterior region; the stylet bulb of the proboscis, with a plate-like muscular wall and a thick layer of glandular cells; the intestinal caecum, with four branches or pouches and two pairs of lateral diverticula; the nervous system, with large ganglion cells in the brain; and a middorsal nerve extending anteriorly beyond the brain.

#### Materials and Methods

Two specimens were collected by dredging, and two were collected at a night light. All four were fixed in Bouin's solution (after being anesthetized by addition of menthol or 70% alcohol). Three of them were sectioned at 10  $\mu\text{m}$  (8  $\mu\text{m}$  for the proboscis apparatus of the holotype), and stained with

Delafield's hematoxylin and eosin. An Olympus or Sony video camera with Symphonic monitor television and Sony color video printer, in addition to an Olympus BH-2 microscope, were used for observation of the material.

*Nipponnemertes fernaldi*, new species  
Figs. 1–9, Tables 1, 2

*Generic diagnosis.*—Monostiliferous hoplomertean with rhynchocoel nearly equal to body length, proboscis sheath composed of a wickerwork of interwoven circular and longitudinal muscles; body wall musculature, especially longitudinal layer, well developed, with layer of diagonal muscles between the circular and the longitudinal muscles, longitudinal musculature not anteriorly divided; stomach with a small diverticulum or caecal folds; intestinal caecum with short anterior diverticula and with lateral diverticula; cerebral sensory organ large and extending behind the dorsal cerebral ganglia; nervous system without neurochords and neurochord cells; accessory lateral nerves absent; blood vascular system with three longitudinal vessels, mid-dorsal vessel with single vascular plug; frontal organ present; cephalic glands well developed but not reaching posteriorly behind the ce-

rebral ganglia, except as lateral bands; excretory system extending from rear of brain to hind regions of foregut; sexes separate.

*Specific diagnosis.*—Pale brown, without pattern; with two pairs of oblique cephalic grooves and dorsomedial longitudinal grooves; each anterior oblique cephalic groove is subdivided by 21 transverse secondary grooves, 14 dorsal to the opening of cerebral organ canal and 7 on the ventrolateral surface of the head below the canal opening; paired posterior oblique cephalic grooves originating at the end of the dorsomedial longitudinal grooves; dorsomedial longitudinal grooves forming anteriorly a pair of epidermal folds; with numerous large ocelli (76 in the holotype, 78 in paratype 1, and 52 in paratype 3) in four groups; dermis thick; rhynchodeum provided with a circular muscle layer; precerebral septum is of the dissolved type composed of separate muscular bundles; proboscis diaphragm provided with central stylet-basis complex, which includes a basis consisting of ovoid body to which the central stylet is attached, columnar structure (with obliquely oriented projection) posterodorsal to it, and more massive posterior portion resting on muscular bolster; stylet bulb with a plate-like muscular wall and a thick layer of glandular cells; 2 or 3 accessory stylet pouches; proboscis with 14 nerves; mouth small and located on the ventral side of the rhynchodeum; esophagus, anterior to brain, surrounded by longitudinal muscle; intestinal caecum with anterior branches or pouches and two pairs of lateral diverticula; intestinal diverticula branched; brain with neurilemma and large ganglion cells; mid-dorsal nerve extending anteriorly beyond the brain; lateral nerve cords with myofibrillae and large efferent nerves; ventral ganglia not distinctly separated from the dorsal ganglia except posteriorly; dorsal ganglia without bifurcated fiber core; paired midgut, foregut, and esophagus nerves originating from the ventral brain; cerebral sensory organ with neurilemma, the cerebral organ canal, located at the anterior end of

the cerebral sensory organ, branching into the medial sensory canal and lateral sac-like canal with two kinds of glandular masses; glands lacking at the bifurcation of the cerebral organ canal; excretory pores lateral to the nerve cords and situated in the posterior portion of the nephridial region.

*Type material.*—Holotype (USNM 1000131), paratype 1 (USNM 1000132), paratype 2 (USNM 1000133) and paratype 3 (USNM 1000134) are deposited at the National Museum of Natural History, Smithsonian Institution, Washington, DC.

The holotype (female) consists mostly of a set of serial sections mounted on 81 slides. These include transverse sections of the anterior portion of the body, midgut, tail, and proboscis, and frontal sections of the proboscis apparatus. The remainder of the holotype consists of short pieces that were not sectioned. Paratype 1 (male) consists of serial sections mounted on 76 slides. These include transverse sections of the anterior portion of the body, midgut, tail, and proboscis, and frontal sections of the proboscis apparatus. Four pieces were not sectioned. Paratype 2 (male) consists of serial sections mounted on 29 slides, which include horizontal sections of the anterior portion of the body and proboscis apparatus, and transverse sections of the tail and two pieces that were not sectioned. Paratype 3 was not sectioned (it dried once after it was preserved).

*Type locality.*—Holotype: Peavine Pass, between Blakely Island and Obstruction Island, Washington, U.S.A. (48°34.7'N, 122°50.5'W); collected on 21 Sep 1964 by dredging, gravel bottom, depth between 42 and 56 m. Paratypes 1 and 2: Friday Harbor, Washington, U.S.A.; collected by night light in water column, depth 4 m on 12 Sep 1964. Paratype 3: Willow Island (48°32.4'N), Washington, U.S.A.; collected on 10 Sep 1964, gravel bottom, depth between 18 and 33 m.

*Etymology.*—The species name commemorates the late Professor Robert Fernald, former Director of Friday Harbor Lab-

oratories of the University of Washington, who collected two specimens (Paratypes 1 and 2).

### Description

*External features.*—The holotype is 5 cm long and 6 mm wide, but 8 mm wide while moving (Fig. 1a, b); paratype 1 is 8 cm long and 7 mm wide anteriorly and 10 mm wide in the midgut region (Fig. 1c, d); paratype 2 is 6 cm long and 8 mm wide; paratype 3 is 4 cm long and 10 mm wide, but 7 cm long and 5 mm wide when narcotized (Fig. 1h–j). The extruded proboscis of the holotype is 2.7 cm long (Fig. 1a). The proboscises of paratypes 1–3 were not extruded when the specimens were preserved. The proboscises of paratypes 1 and 2 were removed from the body for observation of the proboscis apparatus (Fig. 1d). The head is rounded on the anterior margin and slightly separated from the body by a constriction formed by the anterior oblique cephalic grooves.

In the living state, the body is flattened dorsoventrally, convex on the dorsal side, tapering posteriorly to a blunt tip. The color is pale brown on the dorsal surface, and more pale brown on the ventral side, with a colorless lateral margin. In the middorsal portion of the body, the proboscis extends anteroposteriorly within the large rhyncho-coel (Fig. 1b). The brain is recognizable from above as a pair of reddish markings (Fig. 1e, h).

On the dorsal side of the head there are two pairs of oblique cephalic grooves (Fig. 1e, f, h, i). The anterior grooves extend around the margins of the head end and are continued on the ventral surface; they each have 21 short secondary grooves perpendicular to them; 14 of these secondary grooves lie dorsal to the opening of the cerebral organ canal (Fig. 1i) and 7 short secondary grooves lie below the cerebral organ canal opening on the ventrolateral surface of the head. The posterior oblique cephalic grooves are limited to the dorsal side of the

body, and together they form a V-shaped pattern (Fig. 1e, f, h). Two closely parallel longitudinal grooves are located on the mid-dorsal part of the head, as in some species of *Nipponnemertes* and other cratene-mertids. They intersect the anterior oblique cephalic grooves and extend to the posterior oblique cephalic grooves (Fig. 1e, f, h, i). Their course is actually longer than shown in the figures, but their most anterior portions, which extend to the tip of the head, are evident only in transverse sections. In dorsal view, the anterior portion of each dorsomedial longitudinal cephalic groove has a median darkened line due to an epidermal depression that exhibits double epidermal folds in transverse sections (Figs. 1e, f, h, 2a).

The rhynchodeal opening is a slender lengthwise pore on the anteroventral portion of the head (Fig. 1g, j). In both the holotype and paratype 1, the right and left sides of the head region each have up to 39 large ocelli.

*Body wall, musculature, and parenchyma.*—The epidermis is of uniform thickness both in the cephalic region (average 110  $\mu\text{m}$ ) and in the midgut region (average 50  $\mu\text{m}$ ). Large unicellular glands are distributed over the entire body. Small, slender cyanophilous glands are embedded between the large glands.

Two middorsal epidermal folds in the anterior region are separated by a deep median groove (Fig. 2a), but posteriorly the folds unite and the groove disappears. The epidermis of the folds has only a few cyanophilous glands. The secondary grooves of the anterior oblique cephalic grooves, which run perpendicular to the anterior grooves, cut deeply into the epidermis and are distinguished by a thin epithelium free of glands, and also by comparatively long cilia (Fig. 2b).

The dermis, 20  $\mu\text{m}$  to 150  $\mu\text{m}$  thick, is from one-third to three times the thickness of the epidermis. It has fibrils that are predominantly circular, and contains numerous cells with nuclei approximately 4  $\mu\text{m}$  in di-

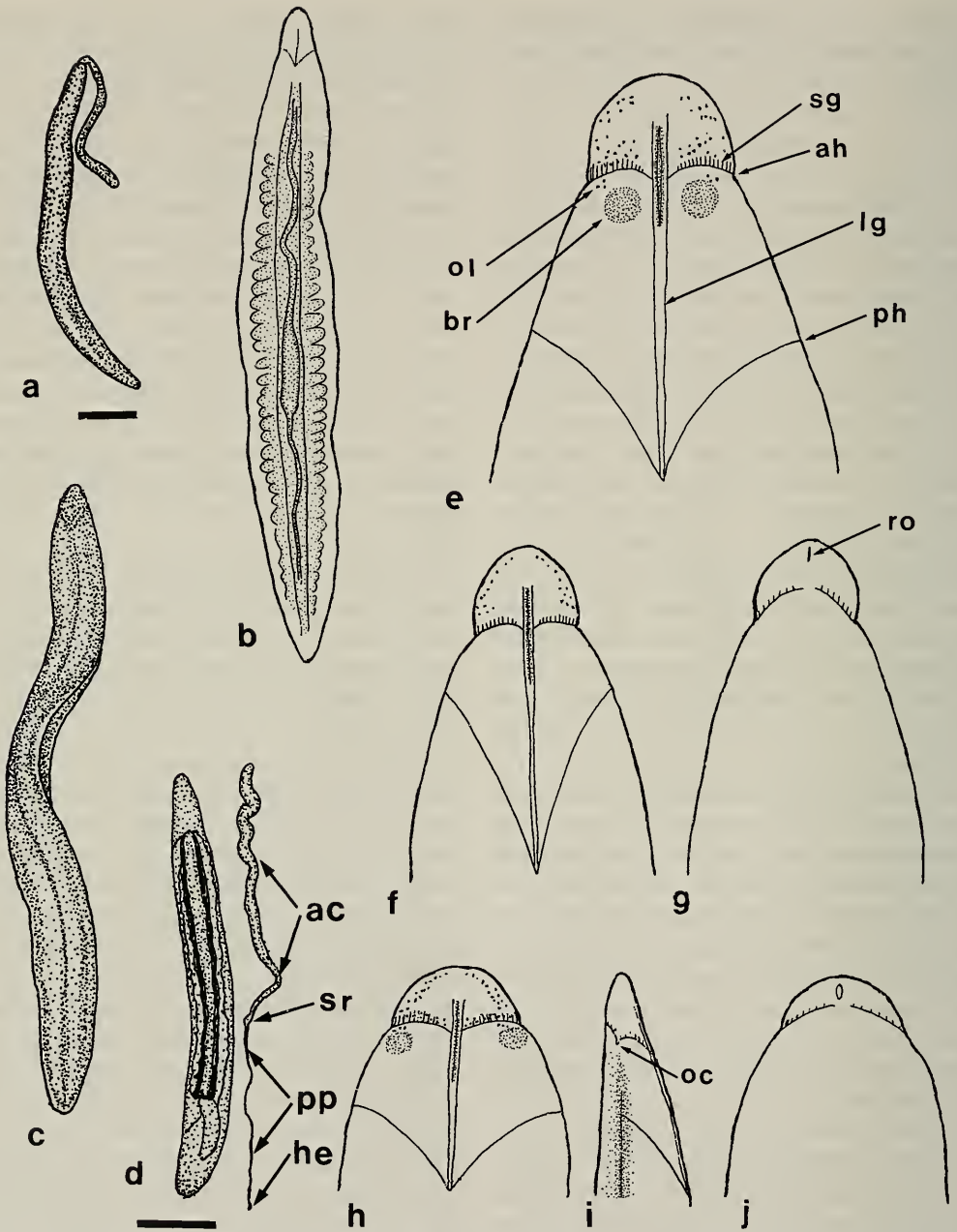


Fig. 1. *Nipponnemertes fernaldi*, new species, external features. (a) holotype, dorsal view; (b) sketch of holotype, dorsal view; (c) paratype 1; (d) paratype 1, and proboscis apparatus; (e) sketch of head of holotype, dorsal view; (f, g) sketches of head of paratype 1 in dorsal and ventral views; (h-j), sketches of head of paratype 3 in dorsal, lateral, and ventral views. Scale = 1 cm (a, d). ac, anterior chamber of proboscis; ah, anterior oblique cephalic groove; br, brain; he, hind end of proboscis; lg, longitudinal cephalic groove; oc, opening of cerebral organ; ol, ocelli behind anterior oblique cephalic groove; ph, posterior oblique cephalic groove; pp, posterior portion of proboscis; ro, rhynchodeal opening; sg, secondary groove; sr, stylet region of proboscis.

ameter (Fig. 2c). Small nerves are found in the dermis.

The body-wall musculature consists of an outer circular layer, inner longitudinal layer, and a recognizable diagonal muscle layer between them (Fig. 2d) (cf. Crandall 1993a). The circular and longitudinal muscle layers extend to the tip of the head, but decrease in thickness precerebrally. The circular layer posterior to the brain region has a fairly uniform thickness of 60  $\mu\text{m}$ . The longitudinal muscle layer consists of bundles arranged perpendicular to the body surface; the dorsal and ventral bundles become thicker (up to 550  $\mu\text{m}$  thick) in the stomach region (Fig. 2e). Longitudinal muscle fibers embedded in the parenchyma of the precerebral region originate from the inner portion of the longitudinal body-wall musculature and extend to the tip of the head. In the precerebral and cerebral region, dorsoventral and radial muscle fibers are not present. Behind the cerebral sensory organs, dorsoventral muscle fibers appear in the parenchyma between the proboscis sheath and the lateral longitudinal body-wall musculature. In the midgut region, well-developed dorsoventral musculature, consisting of crowded fibers, is found between the intestinal diverticula (Fig. 2f). Parenchyma is clearly evident along the lateral sides of the body in the intestinal region.

*Rhynchodeum, rhynchocoel, and proboscis.*—The precerebral region, anterior to the opening of the rhynchodeum, forms a short snout, which is flattened dorsoventrally and contains the ocelli and frontal glands associated with the frontal organ (Fig. 2g). A midventral epidermal groove leads from the rhynchodeal opening to the tip of the snout (Fig. 2g, h). The lining of the groove, forming a narrow median depression, does not differ from the epidermis of the head region, except for a boundary area around the opening of the rhynchodeum, where an epithelium with cilia but without glands is present. The dermis and musculature dorsal to the groove are continuous with those of the remainder of the body wall but are thin-

ner. The longitudinal musculature, however, is displaced by the cephalic glands (Fig. 3a, b).

In paratype 1, the precerebral region does not form a short flattened snout and the mid-ventral groove runs from the tip of the head to the rhynchodeal opening.

The rhynchodeum is lined entirely with a ciliated epithelium without a glandular content. The epithelium rests on a layer of circular musculature 10–50  $\mu\text{m}$  thick in the holotype, 15–150  $\mu\text{m}$  thick in paratype 1; the thickness of the the layer of circular musculature gradually increases toward the posterior end of the rhynchodeum. In the holotype, whose proboscis was extruded, the rhynchodeum is cylindrical and has a length of about 500  $\mu\text{m}$ . Its diameter at the opening measures 350  $\mu\text{m}$ ; at the posterior end it measures 450  $\mu\text{m}$ . At the posterior end of the rhynchodeum, the circular muscle layer around this cavity, properly called the rhynchodeal sphincter, is 50  $\mu\text{m}$  thick; the inner circular muscle layer of the proboscis fuses with it, resulting in compression of the space of the rhynchodeum (Fig. 3b). Part of the fused circular muscle layer measures 120  $\mu\text{m}$  thick, but the thickness decreases posteriorly for about 200  $\mu\text{m}$ , where the fused layer extends transversely to join the circular muscle layer of the body wall (Fig. 3c, d). The inner longitudinal muscle layer of the proboscis, within which the proboscis nerves are situated, becomes thicker posteriorly and forms the precerebral septum of the proboscis apparatus (Fig. 3d, e). Thus the proboscis insertion and the precerebral septum are distinct.

In paratype 1, in which the proboscis was not extruded, the precerebral septum of the proboscis apparatus consists of about 20 loosely arranged bundles of longitudinal muscle. Farther posteriorly, the longitudinal muscles closely surround the thick circular muscle layer around the rhynchodeum.

Posterior to the precerebral septum, a layer about 20  $\mu\text{m}$  thick (Figs. 3e, f, 4c, 7e), in which circular and longitudinal muscu-

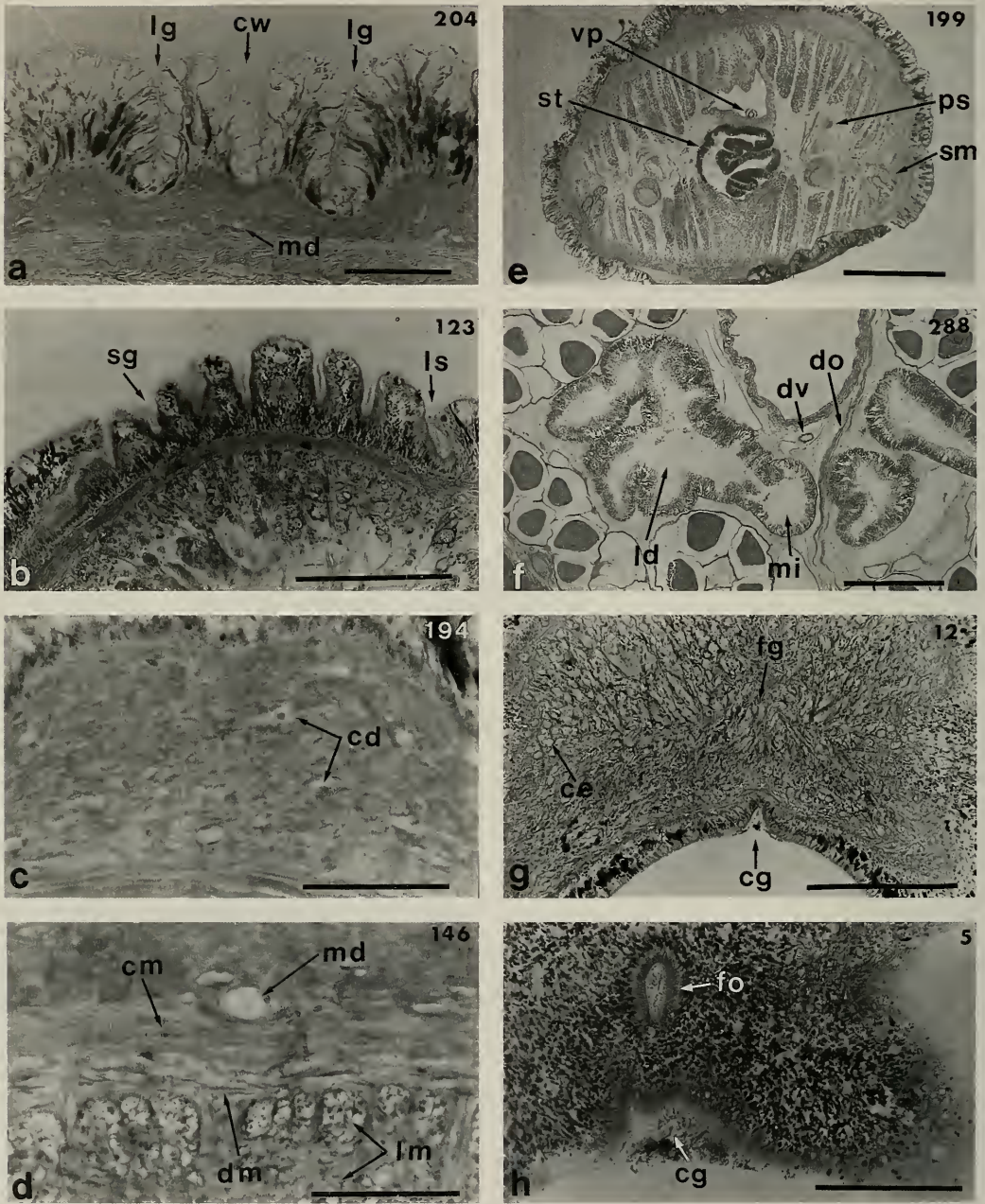


Fig. 2. *Nipponnemerytes fernaldi*, new species. Transverse sections of anterior and middle portions of body, showing (a) two epidermal folds (separated by a central depression) between longitudinal cephalic grooves and a central depression, (b) secondary grooves of anterior oblique cephalic groove (right side), (c) dermis, (d) middorsal nerve and diagonal muscle layer, (e) stomach, (f) midgut and lateral diverticula of midgut, (g) epidermal ciliated groove leading to rhynchodeum, and (h) pit of frontal organ. Scale = 0.5 mm (e, f), 200  $\mu$ m (b, g), 100  $\mu$ m (a), 50  $\mu$ m (c, d). Sections 5–204 from anterior end of body (a–e, g, h); section 288 from anterior end of middle portion of body (f). cd, cell in dermis; ce, cephalic glands; cg, ciliated groove; cm, circular muscle layer of body wall; cw, central depression between mediodorsal longitudinal cephalic grooves; dm, diagonal muscle layer; do, dorsoventral muscle; dv, dorsal blood vessel; fg, frontal gland; fo, frontal organ; ld, lateral diverticulum of midgut; lg, longitudinal cephalic grooves; lm, longitudinal

lature are interwoven, underlies the epithelium of the proboscis sheath.

In paratype 1, the rhynchodeum and esophagus, situated below the cephalic glands, are surrounded by thick bundles of longitudinal musculature and a thin layer of circular muscles.

In the area in which the circular muscle layer of the rhynchodeum and that of the proboscis are united into a thick layer, a coagulated mass of protein-rich rhynchocoel fluid, about 120  $\mu\text{m}$  thick, appears within the proboscis (Fig. 3b, c). The posterior part of this coagulated mass is hollowed out; the space marks the beginning of the rhynchocoel (Fig. 3d, e). The wall of the mass around the space becomes narrower and comes close to the epithelium of the proboscis sheath (Fig. 3g). In paratypes 1 and 2, a mass of coagulated rhynchocoel fluid was not observed (the proboscis was inside the body at the time of preservation).

The rhynchocoel within the proboscis sheath ends a little anterior to the posterior nerve anastomosis. It is narrow in the foregut region, where the longitudinal musculature of the body wall is well developed. The pressure of peripheral tissues causes the rhynchocoel walls to buckle inward into various folds that protrude into the lumen of the rhynchocoel, forming a pair of dorsal and ventral ridges (Figs. 3g, h, 4a, b). In the intestinal region, the rhynchocoel widens and becomes cylindrical (Fig. 4c).

In paratype 1, a pair of small dorsal ridges of the rhynchocoel are present in the cerebral and stomach regions, and a pair of deep ventral ridges also are present at the lateroventral corners of the rhynchocoel.

The structures associated with the central stylet form an unusual complex, as yet not reported for any monostiliferan hoplone-mertean. The following observations are

based on sections of the holotype (Fig. 5a–o). The stylet itself, about 10  $\mu\text{m}$  long, is attached to an ovoid structure in which many small cellular or granular bodies are embedded (Figs. 4d, 5c–e, 6a). This structure, about 25  $\mu\text{m}$  long and 17  $\mu\text{m}$  wide, has a thick, slightly irregular wall. Posterodorsal to it is a nearly columnar, eosinophilous stalk bearing a projection that is oriented obliquely; this has a darkened edge on one side (Figs. 4f, 5g, h, 6a). The stalk is essentially a prolongation of the more massive posterior portion of the basis, about 110  $\mu\text{m}$  long by 80  $\mu\text{m}$  wide. Most of this is stained pale purple, but the nearly conical anterior half of it has a thick coating that is deeply stained purple and has sharp or blunt protuberances, as well as a collar-like ridge that encircles the base of the columnar stalk (Figs. 4f, 5h). The conical portion is free from the tissue surrounding it, but the posterior bulbous part is tightly bound to tissue (Fig. 5f–n).

In paratype 1, the tip of the basis is curved downward and the anterior portion of the central stylet, 17  $\mu\text{m}$  long, is damaged (Fig. 4g). Several large cellular bodies and a few deformed cyanophilous structures are present between the central stylet and the basis. The basis is conical, and its lateral surfaces, stained purplish, have several small and irregular protuberances. One side of the basis faces the ductus ejaculatorius (Stricker & Cloney 1981). In paratype 2, however, the tip of the basis is not curved, and a rectangular body containing a mass of small cyanophilous spheres rests on the tip of the conical portion of the basis (Fig. 4h). The rectangular body, with a wall 5  $\mu\text{m}$  thick, measures 32  $\mu\text{m}$  wide and 37  $\mu\text{m}$  high. The basis is conical, as in the holotype; the free portion of its dorsal side has

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muscle layer of body wall; ls, most lateral groove on lateral side of head; md, middorsal nerve; mi, midgut; ps, posterior end of cerebral sensory organ; sg, secondary groove; sm, submuscular gland; st, stomach; vp, vascular plug inside proboscis sheath.

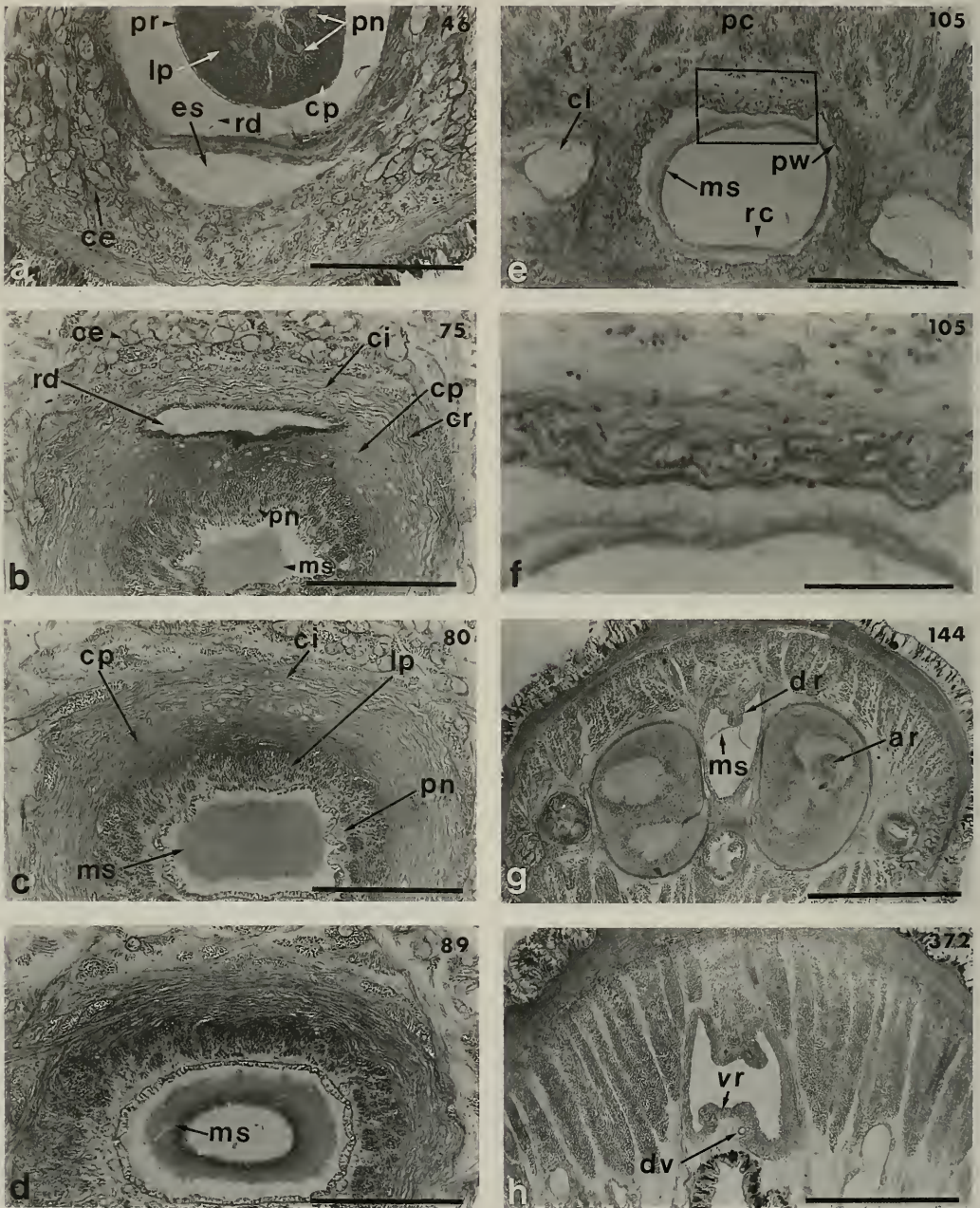


Fig. 3. *Nipponnemertes fernaldi*, new species. Transverse sections of anterior portion of body, showing (a) flattened portion of esophagus under rhynchodeum, (b) tight connection of circular muscle layer of rhynchodeum to that of proboscis, (c) united circular muscle layers of rhynchodeum and proboscis, (d) reduction of thickness of united circular muscle layers running laterally to circular muscle layer of body wall, (e) formation of pre-cerebral septum from longitudinal muscle layer of proboscis, (f) enlarged proboscis sheath formed from epithelium of proboscis, and (g, h) successive changes in shape of rhynchocoel. Scale = 0.5 mm (g, h), 200  $\mu$ m (a–e) and 50  $\mu$ m (f). 46–372, numbers of sections from anterior end of body. ar, artifact; ce, cephalic glands; ci, circular muscle layer of rhynchodeum; cl, cephalic blood lacuna; cp, circular muscle layer of proboscis; cr, circular muscle layer of rhynchodeum united to that of proboscis; dr, dorsal ridge of proboscis sheath; dv, dorsal blood vessel; es, esophagus; lp, longitudinal muscle layer of proboscis; ms, membranous sheath of coagulated



purplish edges, but lacks protuberances. In paratype 2, the central stylet is lacking.

The basis rests on a large bolster consisting of interwoven circular and longitudinal muscle (Fig. 4e). It is 110  $\mu\text{m}$  long medially, 150  $\mu\text{m}$  long laterally, and 370  $\mu\text{m}$  wide. The basis is surrounded by circular and longitudinal muscle bundles extending dorsally from the bolster. This muscular arrangement continues beyond the basis to the middle area of the stylet column, which extends from the tip of the proboscis to the central stylet of the proboscis apparatus (Fig. 4e). Posterior to the basis, the bolster is divided into two parts, with a space between. The bolster, basis, and muscular wall are continuous with the wall of the middle part of the proboscis. The clusters of eosinophilous glands of the proboscis epithelium are evident at the anterior end of this organ (Fig. 4e).

Posterior to the bolster, there is a large bulb-like structure called the dilated ampulla or stylet bulb (Stricker 1985) (Fig. 4e); its wall is about 50  $\mu\text{m}$  thick, and consists of interlacing circular muscles, thick connective tissue, a plate-like muscular wall on its anterior side, and a thick layer of glandular cells. In *Nipponnemertes punctatulus* and *N. bimaculatus* (reported by Iwata 1951, 1954), the platelike muscular wall and the thick layer of glandular cells were not found. In the area where a space is formed between the two halves of the divided bolster, the muscular anterior plate of the bulb is extended forward, and a narrow duct called the ductus ejaculatorius connects the interior of the stylet bulb with the space. On the posterior side of the bulb, a narrow canal leads to the posterior chamber of the proboscis (Fig. 7a).

In the holotype and paratype 1, two large pouches of accessory stylets are situated an-

terior to the central stylet, between the outer epithelium and the muscular wall of the bolster (Figs. 4e, 5a). Through a narrow curved duct, each pouch, measuring 265  $\mu\text{m}$  dorsoventrally, 230  $\mu\text{m}$  long, and 170  $\mu\text{m}$  wide, opens into the lumen of a canal that is directed upward from the basis. In each pouch, there are four accessory stylets, about 10  $\mu\text{m}$  long; they lie in vesicles about 30  $\mu\text{m}$  by 20  $\mu\text{m}$  (Figs. 4e, 5a). In paratype 2, there are three pouches of accessory stylets, and the number of stylets is 6, 8, and 8, respectively.

The proboscis has an outer circular and inner longitudinal muscle layer (Fig. 3a, c); there are 14 nerves within the proboscis in the holotype and paratype 1.

*Alimentary canal.*—The alimentary canal has five major divisions: esophagus, stomach, pylorus, midgut (with anteriorly directed caecum and lateral diverticula), and hindgut. The mouth is small and on the ventral side of the head close to the rhynchodeal opening (Fig. 7b). The distance between the rhynchodeal opening and the mouth is 150  $\mu\text{m}$  in the holotype, 200  $\mu\text{m}$  in paratype 1. Neither the esophagus nor the stomach has longitudinal or circular musculature; the shape of the esophagus is influenced by the longitudinal musculature of the body wall, situated on its dorsal and lateral sides. The esophagus soon flattens dorsoventrally (Fig. 3a). At first its epithelium is very thin but then thickens. It is not ciliated, but middorsally it has a mass of gland cells projecting inward. Near the level of the midventral portion of the brain, the esophagus widens and develops two folds; these mark the transition into the stomach. The first fold incorporates some of the glandular cells. The stomach epithelium, in which eosinophilous gland cells begin to predominate, has two folds that are contin-

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fluid; pc, precerebral septum of proboscis apparatus; pn, proboscis nerves; pr, proboscis in rhynchodeum; pw, proboscis sheath, consisting of interwoven circular and longitudinal muscles; rc, rhynchocoel; rd, rhynchodeum; vr, ventral ridge of proboscis sheath.

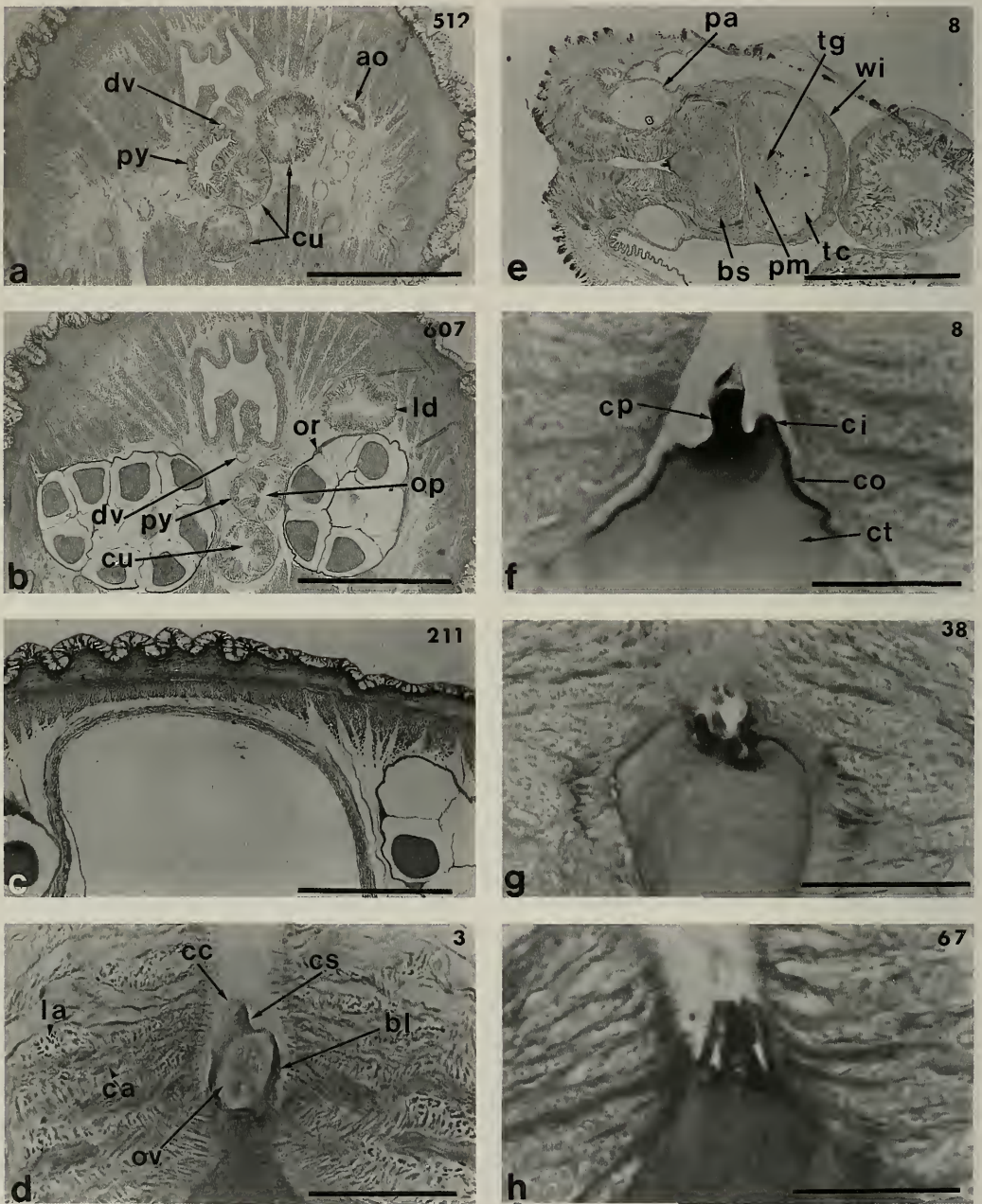


Fig. 4. *Nipponnemertes fernaldi*, new species. Transverse sections of anterior and middle portions of body, showing (a-c) successive changes in shape of rhynchoeol, (d) central stylet on ovoid anterior portion of basis in the holotype specimen, (e) columnar portion of basis in the holotype specimen, (f) central stylet damaged in shape in the specimen of paratype 1, (g) rectangular anterior portion of basis in the specimen of paratype 2, (h) anterior end of proboscis extruded outside, showing proboscis apparatus in the holotype specimen. Scale = 0.5 mm (a-c, e), 200  $\mu$ m (f, g) and 50  $\mu$ m (d, f-h). 3, 8, 38, and 67, number of sections of proboscis apparatus (d-h); 512 and 607, numbers of sections from anterior end of body (a, b); 211, section from middle portion of body (c). ao, anterior end of ovaries; bl, bulb-like basis of central stylet; bs, bolster; ca, circular muscle bundle of proboscis sheath; cc, cover of stylet; ci, collar-like ridge of massive posterior portion of basis (the ridge encircles the columnar portion of the basis); co, nearly conical part of posterior portion of basis, free of sur-

uous with those of the esophagus, as in most species of *Nipponnemertes*. At the level of the posterior end of the cerebral sensory organs, the stomach enlarges and develops a third fold (Fig. 2e). Over most of its length, the stomach is more than twice as wide as it is where it joins the esophagus (Fig. 2e). Beneath the stomach is a substantial mass of longitudinal body-wall muscle (Fig. 2e). Measured from the anterodorsal to posteroventral limits of the gastric folds, the stomach is about three times as long as the brain.

In the holotype, the pylorus, which follows the stomach, is about 1.5 mm long and about two and one-half times as long as the stomach. It originates from the right side of the stomach, between its lateral wall and its principal fold. The left side of the stomach continues posteriorly into a diverticulum formed as an artifact of contraction (Fig. 7c). The pylorus is oval in transverse section; it is about 0.25 mm wide at its junction with the stomach, and narrows to 0.15 mm at the point where it opens into the midgut (Fig. 4b). Its ciliated epithelium contains cyanophilous gland cells and is thus different from the lining of the postero-dorsal area of the gastric cavity (Fig. 7d).

In paratype 1, the pylorus is about 4 mm long and about three times as long as the stomach. The diverticulum of the stomach, about 0.6 mm long, has three caecal folds in its outer portion.

In the holotype, the intestinal caecum has four anterior tubular branches, of which three arise from the main caecum (Fig. 6b). Posteriorly, it has two pairs of lateral diverticula; those of the anterior pair are of unequal length and are parallel to the main caecum. Those of the posterior pair form a tube connected by a short duct to the main

caecum; this tube extends posteriorly beyond the pylorus. The intestinal caecum and anterior branches extend anteriorly for about half the length of the pylorus.

In paratype 1, the intestinal caecum has four anterior pouches that originate from the main caecum just anterior to where the first pair of lateral diverticula branch off; the main caecum does not extend any farther anteriorly. The intestinal caecum, about 1.5 mm long, extends anteriorly above the posterior portion of the pylorus for less than half its length.

Most of the lateral diverticula of the anterior part of the intestine are divided into dorsal and ventral lobes (Fig. 2f); the lobes are unequal and variable in number and length. The epithelium of the intestine contains eosinophilous gland cells. In the holotype, this part of the digestive tract, circular in transverse sections, does not have its own musculature, but in paratype 1, there are a few circular muscles in the wall of the intestine.

In paratype 2, the anus opens ventrally near the posterior end of the body. It is a slit about 100  $\mu\text{m}$  long, and has an inside diameter of 30  $\mu\text{m}$  transversely and 15  $\mu\text{m}$  dorsoventrally. The wall is 40  $\mu\text{m}$  thick. The rectum is 140  $\mu\text{m}$  long and is surrounded by a circular muscle layer 50  $\mu\text{m}$  thick. In paratype 1, the rectum has the same structure as in paratype 2. In the holotype, the series of sections of the posterior portion of the body is not complete.

*Blood-vascular system.*—The blood vascular system has three longitudinal vessels. The two cephalic blood vessels lateral to the rhynchodeum anastomose above the rhynchodeum near the tip of the head to form the cephalic loop. Farther posteriorly, however, the cephalic vessels become large

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rounding tissue; cp, columnar portion of basis; cs, central stylet; ct, bulbous part of posterior portion of basis, tightly bound to tissue; cu, intestinal caecum; dv, dorsal blood vessel; la, longitudinal muscle bundle of proboscis sheath; ld, lateral diverticula of midgut; op, opening of pylorus; or, ovary; ov, ovoid anterior portion of basis; pa, pouch of accessory stylet; pm, platelike muscular wall; py, pylorus; tc, dense connective tissue; tg, dense layer of glandular cells; wi, stylet bulb-wall consisting of circular muscle.

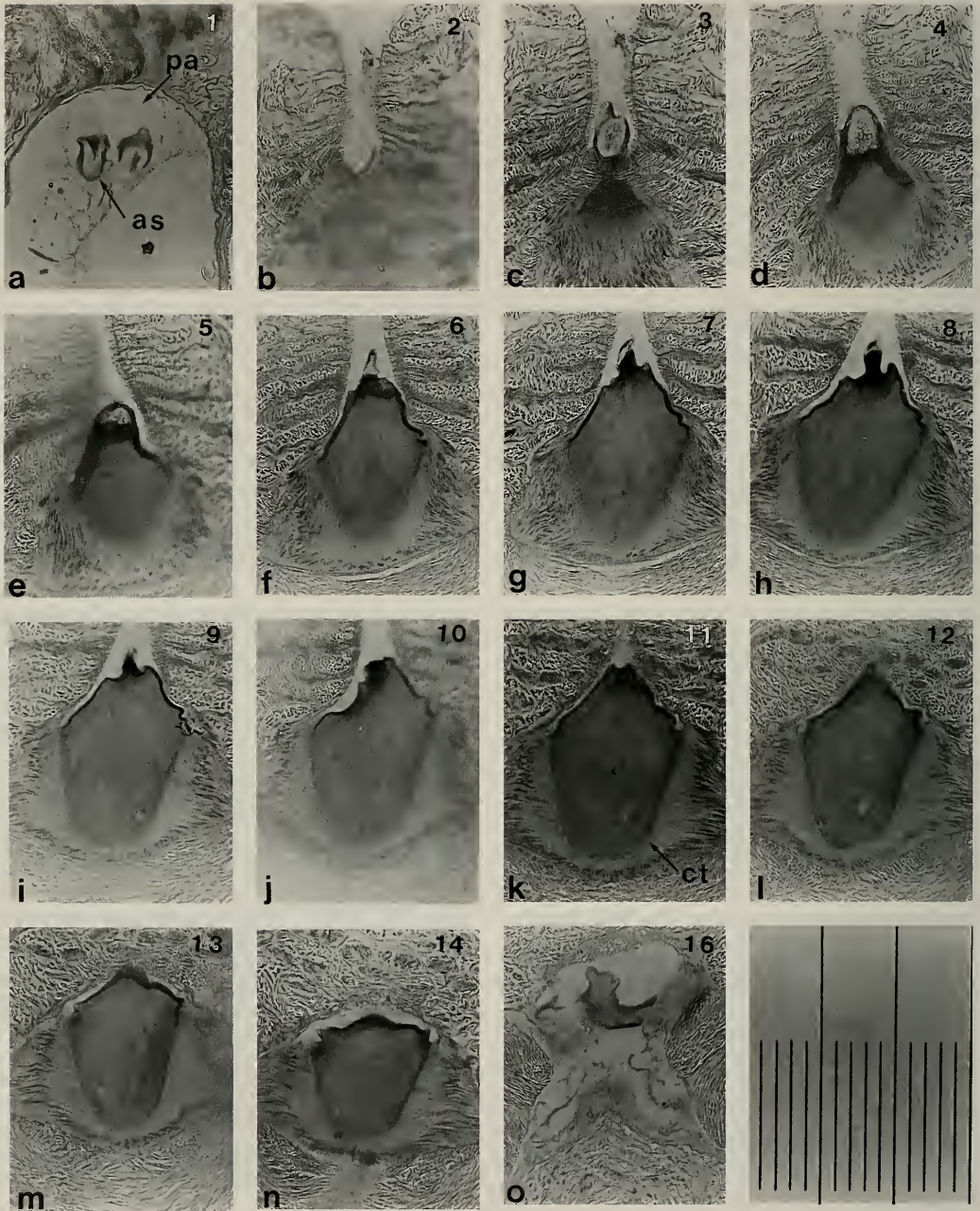


Fig. 5. *Nipponnemertes fernaldi*, new species. Successive transverse sections of proboscis apparatus in the holotype specimen (a-o), showing especially accessory stylet (a), bulbous proboscis vesicle (c-e), and obliquely oriented projection of columnar portion of basis (f-i). Scale = 150  $\mu$ m, 1-16, numbers of sections of proboscis apparatus. as, accessory stylet; ct, bulbous part of posterior portion of basis; pa, pouch of accessory stylelets.

lacunae that turn medially in front of the brain. At the level of the anterior end of the ventral ganglia, they become narrowed into vessels that enter the brain ring without giving off cerebral vessels and then run alongside the rhynchocoel (Fig. 3g). In the holotype, the right vessel soon communicates with the dorsal vessel, which then enters the proboscis sheath, at the level of the posterior end of the brain, as a single median vascular plug, and extends medioventrally in the sheath as far as the anterior pyloric region, a distance of about 1.4 mm (Figs. 2e, 7c–e, g, 8e). This portion of the vascular plug seems to form a specialized communication with the rhynchocoel (Fig. 7e). After passing ventrally out of the rhynchocoel, the dorsal vessel continues posteriorly under the proboscis sheath between the rhynchocoel and the alimentary canal (Figs. 2f, 3h, 4a, b). In paratype 1, however, it is the left vessel that communicates with the dorsal vessel at the level of the posterior portion of the cerebral sensory organs or behind the brain, and the single median vascular plug extends as far as the middle pyloric region, a distance of about 3.1 mm.

Behind the cerebral organs, the lateral vessels enter the nephridial region, which extends from the posterior end of the cerebral organs to the level of the anterior portion of the pylorus (in the holotype) or to the level of the anterior portion of the intestine (in paratype 1) (Figs. 4a, 7c, d, f); there the vessels are dorsal to the lateral nerve cords.

Transverse anastomoses of the lateral vessels in the intestinal region were not observed.

In both paratype 1 and 2, the dorsal and lateral vessels anastomose just above the posterior end of the rectum, where a commissure of the lateral nerves and the end of the rhynchocoel come together at the same transverse level.

*Nervous system.*—The brain is situated immediately behind the large cephalic lacunae. The right lacuna is 340  $\mu\text{m}$  wide and 100  $\mu\text{m}$  high. The dorsal and ventral gan-

glia are not demarcated externally. The ventral commissure of the brain is situated near the anterior end of the brain and the ventral ganglia are not distinctly separated from the dorsal ganglia, except posteriorly. They become completely separated for a distance of 30  $\mu\text{m}$ . (Figs. 6c, 7g). The dorsal and ventral fiber cores are not divided anterior to the middle portion of the brain; the dorsal cores are more voluminous than the ventral cores. The dorsal ganglia do not extend as far posteriorly as the ventral ganglia, and dorsal and ventral lobes are lacking (Fig. 6c). A thick nerve cord from the posterior end of each dorsal ganglion enters the corresponding cerebral sensory organ (Figs. 6c, 7g). A long, thin dorsal commissure (40  $\mu\text{m}$  thick), and a short, much thicker ventral commissure (110  $\mu\text{m}$  thick), connect the right and left ganglia at about the same transverse level (Fig. 6c). In paratype 1, however, the dorsal commissure (70  $\mu\text{m}$  thick) is situated a short distance (30  $\mu\text{m}$ ) farther anterior than the ventral one (130  $\mu\text{m}$ ). The dorsal commissure curves upward to lie above the dorsal ridge of the proboscis sheath. On both sides, the brain is in contact with the dorsolateral wall of the esophagus, which is spanned dorsally by the ventral commissure. The brain and lateral nerves are covered by a thin neurilemma and a thick layer of fibrous connective tissue (Fig. 7h). In the intestinal region, however, the neurilemma of the lateral nerves is not evident. In the cerebral fiber core of each dorsal ganglion, there are numerous large cellular bodies (Fig. 8a, b), similar to those in *Nipponnemertes punctatulus* (reported by Iwata 1951) (Fig. 9c, d) and the reptant polystyliferan *Kameginemertes parmiornatus* (Iwata 1998). The structure of these cellular bodies is not clearly defined.

In the mass formed by the dorsal and ventral ganglia, there is, in the outer part of the right side of the brain, a large ganglion cell 20  $\mu\text{m}$  long; its nucleus measures 6  $\mu\text{m}$ . It is situated immediately behind the ventral commissure (Fig. 8c). A large gan-

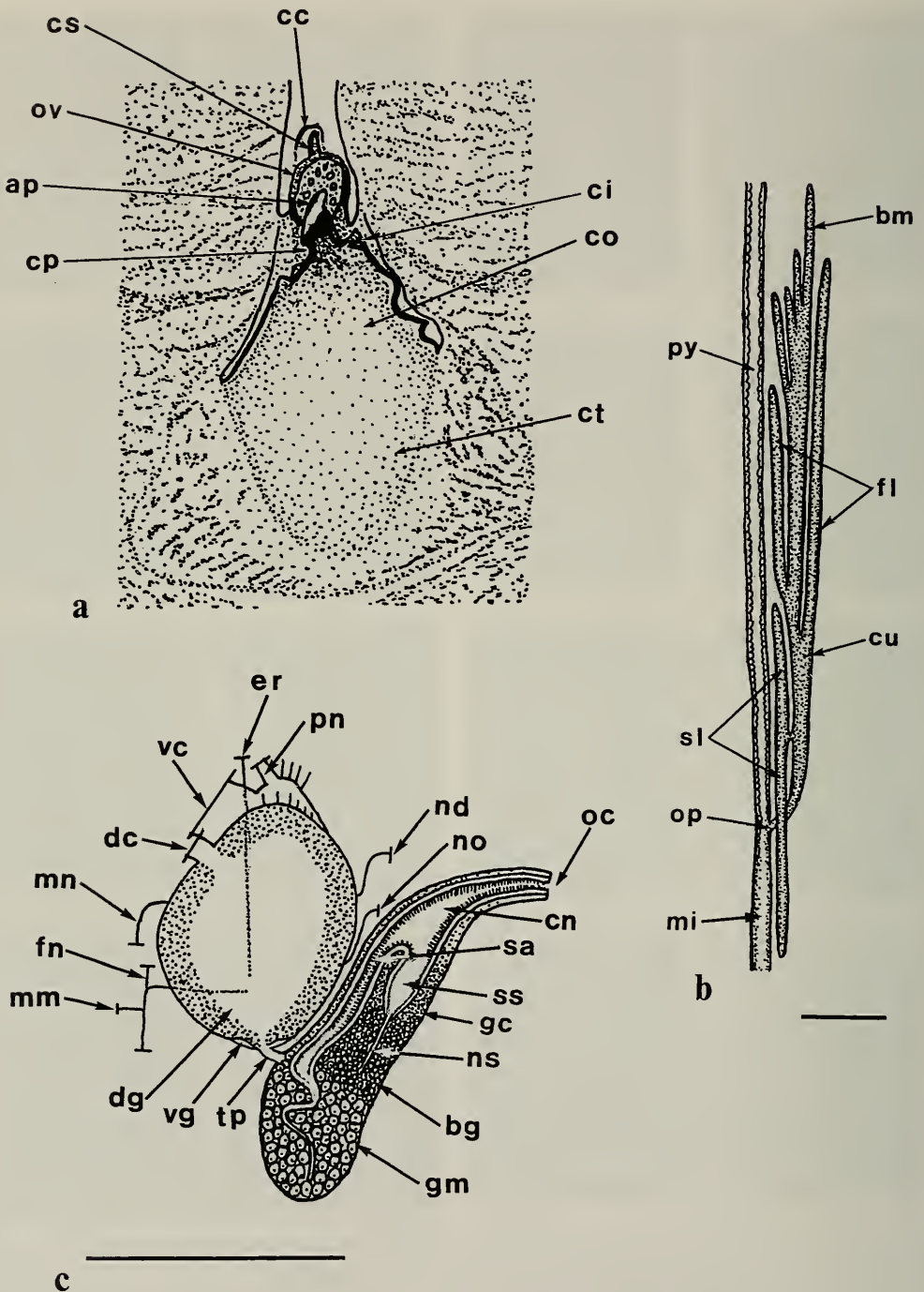


Fig. 6. *Nipponnemertes fernaldi*, new species. (a) Drawing of frontal sections of central stylet-basis complex of proboscis, (b) Drawing of dorsal view of caecum of midgut and pylorus, arranged laterally to the caecum of midgut, showing four branches and two pairs of tubular lateral diverticula, and (c) Drawing of dorsal view of brain and cerebral sensory organ (right side) showing relationships of these structure. Scale = 200  $\mu$ m (b) and 0.5 mm (c). ap, obliquely oriented projection of columnar portion of basis; bg, cyanophilous glandular mass of saclike canal; bm, branch of midgut caecum; cc, cover of central stylet; ci, collar-like ridge of massive posterior

gion cell on the left side was not observed. In paratype 1, large ganglion cells, 20  $\mu\text{m}$  long and containing nuclei measuring 10  $\mu\text{m}$ , lie medially in the brain, in the region of the ventral commissure (left) or behind it (right). It appears that the ganglion cells in this species are identical to Bürger type-3 ganglion cells, which are found in several cratenemertids (Bürger 1895). In the heteronemertean *Micrura leidyi*, Riser (1998) demonstrated a neurochord cell in the ganglionic layer of each ventral lobe of the brain and additional neurochord cells in the lateral nerve cords. His photomicrograph shows features similar to those of the large ganglion cell of *N. fernaldi*, but neurochords are lacking in both the brain and lateral nerve cords of this species.

In the intestinal region, the lateral nerve cords, ventrolateral in position, lie above the longitudinal musculature of the body wall, and they give off dorsal or dorsoventral peripheral nerves that extend toward the dorsal and ventral sides of the body (Fig. 8d).

Several slender but conspicuous nerves originate from the brain (Fig. 6c). They branch out pre- and post-cerebrally to supply various structures. A proboscis nerve trunk arises from the anterior side of each ventral ganglion and immediately extends to the proboscis sheath. Both proboscis nerves soon branch into seven nerves that lie on the lateral side of the sheath. Three small cephalic nerves, arranged one above the other and parallel to the proboscis nerve trunks, emerge from the anterior face of each ventral ganglion and proceed anteriorly

only on the ventral side of the cephalic region. Six small cephalic nerves originate from the dorsal ganglion a little farther posteriorly than the cephalic nerves on the ventral side, and they extend precerebrally to supply the eyes. A small nerve from each ventral ganglion extends anteriorly and then turns toward the outer side of the head, entering the dermis after passing the ventral side of the cerebral organ canal. A conspicuous nerve originates from the lateral surface of each ventral ganglion and runs anteriorly; its branches supply the oblique cephalic grooves. A small nerve from the lateral side of each dorsal ganglion extends anteriorly for a short distance and turns toward the lateral side of the head, innervating the ocelli of the most posterior group.

The midgut nerves originating from the medial side of each ventral ganglion run between the ventral ganglia and the foregut, extending posteriorly along the dorsolateral portion of the foregut (Figs. 6c, 8e). The foregut nerves are a conspicuous feature of this species. They emerge on the ventral wall of the ventral ganglion, continue along the lateral side of the foregut, and have a commissure under the esophagus (Fig. 8e). The esophagus nerves, under the rhynchodeum, emanate from the ventral surface of the ventral ganglia and extend anteriorly along the lateral sides of the esophagus, reaching beyond the brain.

Three nerves, originating from the ventral side of each ventral ganglion, separately control different regions of the gut. One runs beneath the rhynchodeum and the anterior part of the esophagus; one innervates

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portion of basis (the ridge encircles the columnar portion of the basis); cn, cerebral organ canal; co, conical part of posterior portion of basis, free of surrounding tissue; cp, columnar portion of basis; cs, central stylet; ct, bulbous part of posterior portion of basis, tightly bound to tissue; cu, caecum of midgut; dc, dorsal commissure of brain; dg, dorsal ganglion; er, esophagus nerve; fl, first pair of lateral diverticula of midgut caecum; fn, foregut nerve; gc, ganglionic mass of cerebral ganglion; gm, eosinophilous glandular mass of sensory canal; mi, midgut; mm, commissure of foregut nerve; mn, midgut nerve; nd, nerve to dermis; no, nerve to ocelli; ns, narrow duct of sa-like canal; oc, opening of cerebral organ; op, opening of pylorus; ov, ovoid anterior portion of basis; pn, proboscis nerve; py, pylorus; sa, sensory canal; sl, secondary pair of lateral diverticula of midgut-caecum; ss, sac-type canal; tp, thick nerve from dorsal ganglion; vc, ventral commissure of brain; vg, ventral ganglion.

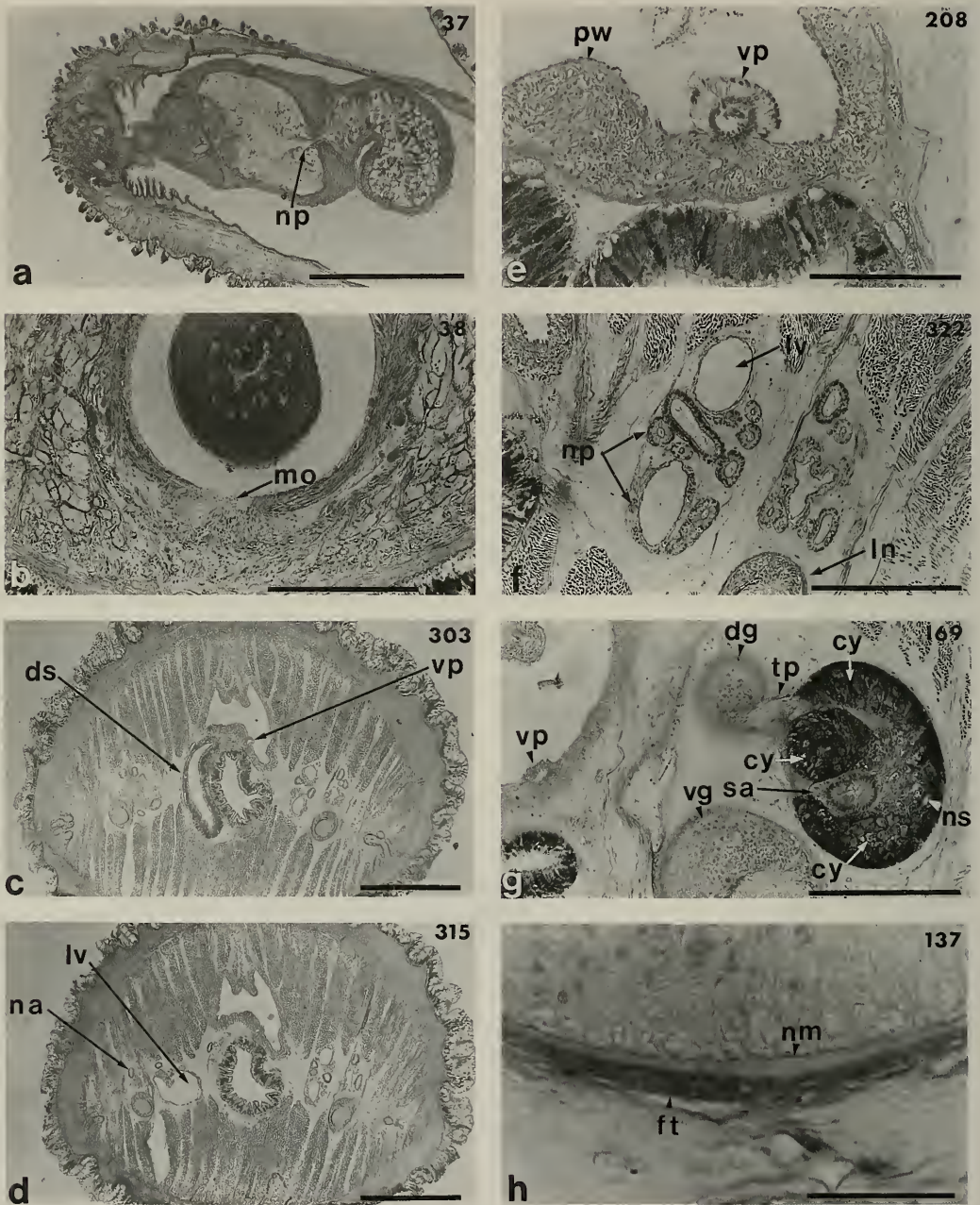


Fig. 7. *Nipponnemertes fernaldi*, new species. Transverse section of proboscis apparatus in the holotype specimen (a), showing narrow canal in thick connective tissue of stylet bulb. Transverse sections of anterior portion of body, showing (b) mouth opening to rhynchodeum, (c) diverticulum of stomach, (d) pylorus, (e) vascular plug inside proboscis sheath, (f) nephridium, (g) thick nerve from dorsal ganglion to cerebral sensory organ, and (h) neurilemma and fibrous connective tissue of brain. Scale = 0.5 mm (a, c, d, h), 200  $\mu$ m (b, f, g), 100  $\mu$ m (e) and 50  $\mu$ m (h). 37, number of section of proboscis apparatus (a) and 38–315; numbers of sections from anterior end of body (b–h). dg, dorsal ganglion; ds, diverticulum of stomach; ft, fibrous connective tissue; ln, lateral nerve; lv, lateral blood vessel; mo, mouth; na, nephridium; nm, neurilemma; np, narrow canal in thick connective tissue and muscular wall of stylet bulb; ns, narrow duct of sac-type canal; pw, proboscis sheath, consisting of interwoven circular and longitudinal muscles; tp, thick nerve from dorsal ganglion; vg, ventral ganglion; vp, vascular plug inside proboscis sheath.



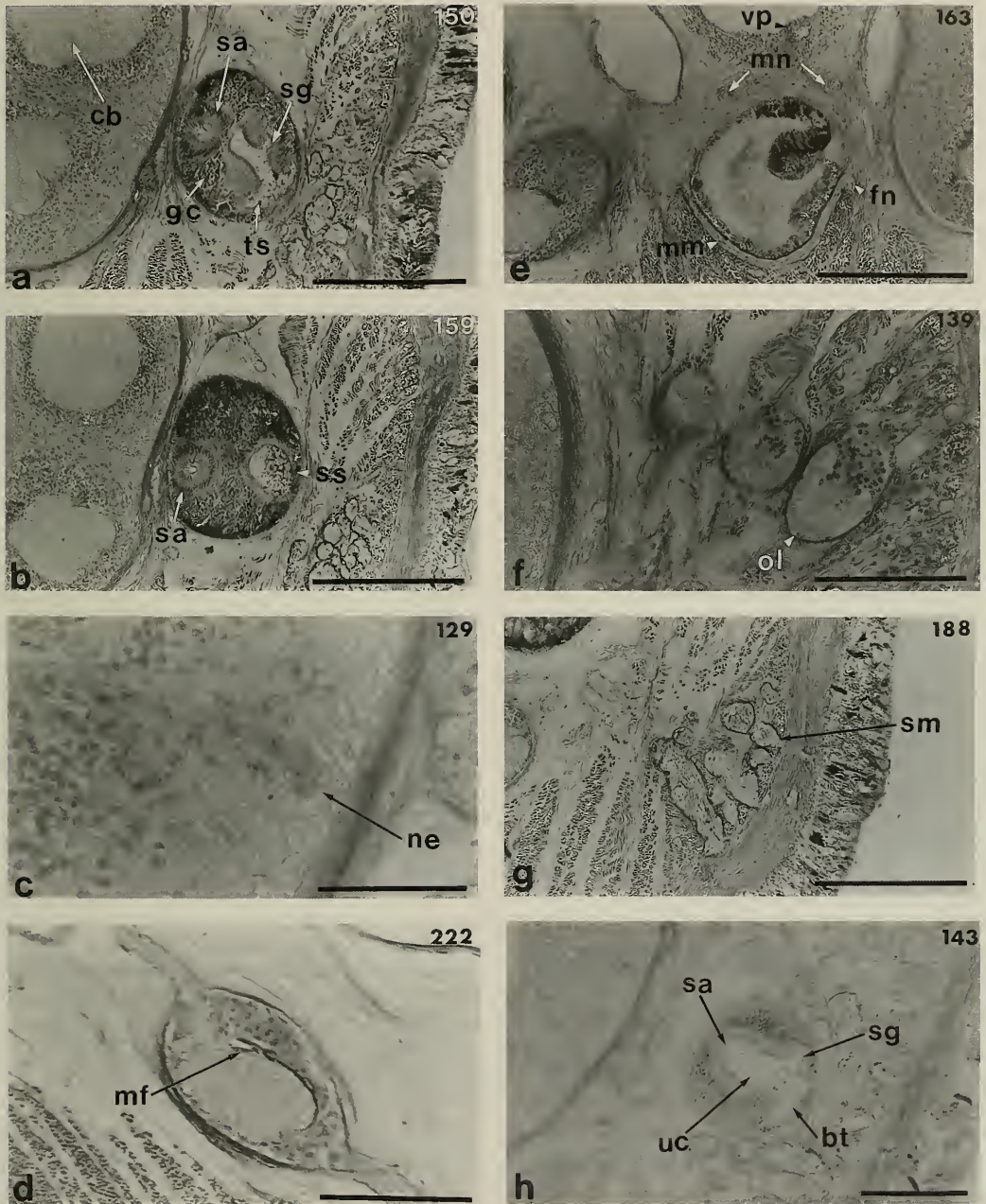


Fig. 8. *Nipponnemertes fernaldi*, new species. Transverse sections of anterior portion of body, showing (a, b) sensory canal and saclike canal after separation from cerebral organ canal, (c) large ganglion cell, (d) lateral nerve cord, (e) nephridium, (f) ocelli, (g) submuscular gland, and (h) posterior end of cerebral organ canal. Scale = 200  $\mu\text{m}$  (a, b, e, g), 100  $\mu\text{m}$  (d, f, h) and 50  $\mu\text{m}$  (c). 129–188, numbers of sections from anterior end of body (a–c, e–h); 222, number of section from anterior end of middle portion of body (d). bt, beginning of T-shaped canal; cb, cellular body in dorsal ganglion; fn, foregut nerve; gc, ganglionic mass of cerebral sensory organ; mf, myofibril; mm, commissure of foregut nerve; mn, midgut nerve; ne, large ganglion cell; ol, ocelli; sa, sensory canal; sg, shallow lateral groove; sm, submuscular gland; ss, sac-like canal; ts, sac epithelium; uc, U-shaped ciliated sensory portion; vp, vascular plug inside proboscis sheath.

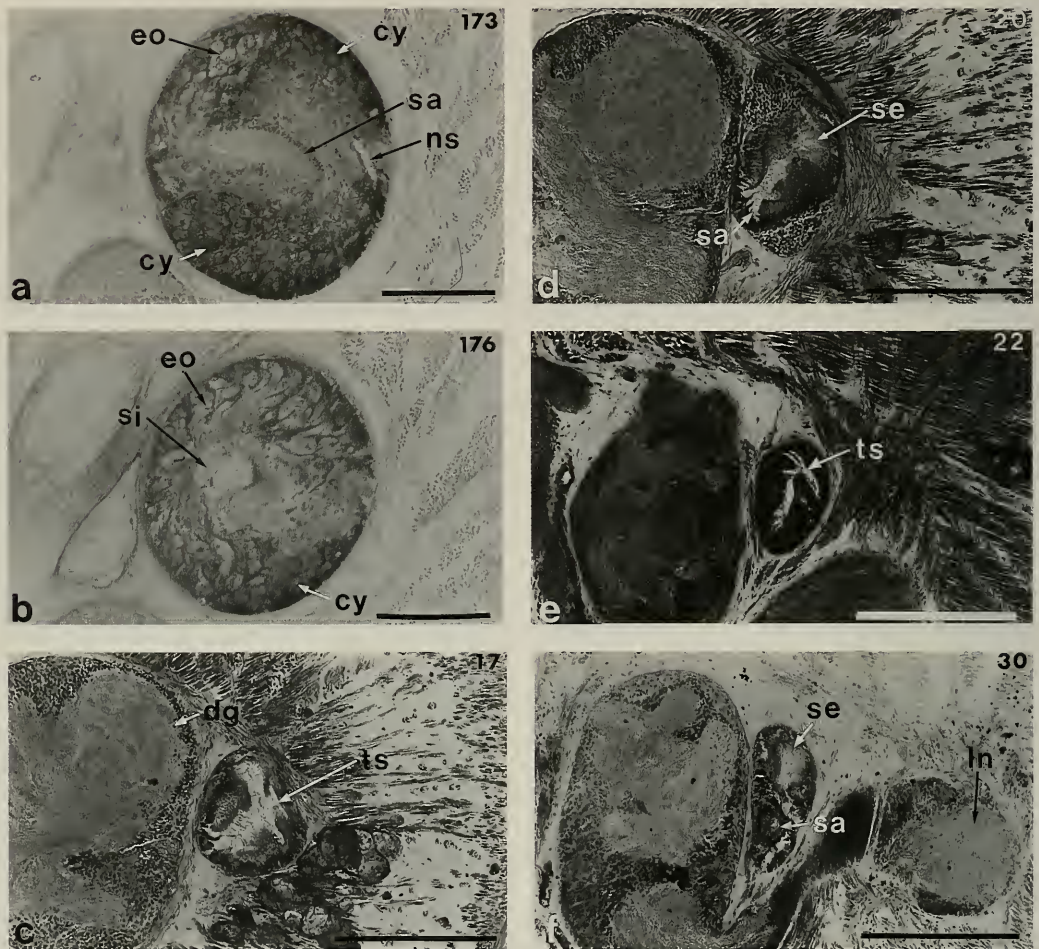


Fig. 9. *Nipponnemertes fernaldi*, new species. Transverse sections of posterior portion of cerebral sensory organ. *Nipponnemertes bimaculatus*, transverse sections showing (c) sensory canal and sac (lumen T-shaped) and (d) sensory canal and sac without epithelium. *Nipponnemertes punctatulus*, transverse sections showing (e) sensory canal and sac (lumen T-shaped) and (f) sensory canal and sac without epithelium. Scale = 200  $\mu\text{m}$  (d–f) and 50  $\mu\text{m}$  (a, b). 173 and 176, numbers of sections from anterior end of body; 17, 20 and 22, 30, numbers of sections of proboscis apparatus (c–f). cy, cyanophilous glandular mass; dg, dorsal ganglion; eo, eosinophilous glandular mass; ln, lateral nerve; ns, narrow duct of sac-like canal; sa, sensory canal; se, sac; si, sensory canal in eosinophilous glandular mass; ts, sac epithelium with T-shaped lumen.

the posterior part of the esophagus, as well as the stomach and pylorus; the last innervates the midgut.

The middorsal nerve lies in the dermis just above the circular muscle layer of the body wall and extends beyond the brain anteriorly, below the dorsomedial longitudinal grooves (Fig. 2d). Its origin from the dorsal commissure of the brain was observed in paratype 1 but was not clear in the holotype. The lateral nerves, with myofibrillae,

give off peripheral nerves and are posteriorly connected to each other by a commissure on the dorsal side of the rectum (Fig. 8d). Myofibrillae in the lateral nerves are situated on the dorsal side between the outer ganglion mass and the inner fibrous core. Myofibrillae have been described for some members of the Cratenemertidae (Crandall 1993a, b; Crandall & Gibson 1998; Riser 1998).

*Special sensory organs and frontal or-*

*gan.*—In the holotype, the ocelli, counted in transverse sections of the head, number 76. They are large and confined to the area between the flattened anterior end of the head and the middle region of the brain. There are 34 ocelli on the right side of the head and 35 on the left. Two groups on each side are recognizable; one consists of 23 (right) and 24 (left) ocelli lateral to the rhynchodeum, and the second consists of 11 (right and left) ocelli; three (right) and four (left) near the middle region of the brain are arranged dorsoventrally along the lateral sides of the head (Fig. 8f).

In paratype 1, there are 78 ocelli, 39 on both sides. Of the two groups on the right side; one consists of 22 ocelli, and the other consists of 14; of the two groups on the left side, one consists of 25 ocelli, the other consists of 11. Three ocelli (right and left) near the middle region of the brain are arranged as in the holotype specimen. In paratype 3 (Fig. 1h), there are 52 ocelli, 26 on both sides. 13 are marginal, 10 are on the anterior oblique cephalic grooves, and 3 are behind it. The arrangement of ocelli in paratype 2 was not studied.

The ocelli are of the inverted pigment-cup type and have dimensions of up to 90  $\mu\text{m}$  wide and 110  $\mu\text{m}$  high (Fig. 8f).

The cluster of frontal gland cells, which fan out into separate strands in the dorsal side of the head, is not large. In both the holotype and paratype 1 the cluster extends to the region of the proboscis insertion without reaching posteriorly to the cerebral ganglia (Figs. 3a–c, 7b). The frontal glands deliver their secretions to a pit at the anterior tip of the snout (Fig. 2g, h). The pit represents a frontal organ.

The cephalic glands, confined to the lateral sides of the head, are found close to the frontal glands. The lateral bands of mucoid glands are posterior extensions of the cephalic glands. Below the frontal organ, there is a narrow and short ciliated groove running posteriorly to the dorsal side of the rhynchodeal opening (Fig. 2g, h). In para-

type 1, this groove continues to the opening of the rhynchodeum.

The posterior extensions of the mucoid cephalic glands, namely the submuscular glands, are situated laterally in the foregut region, beginning at the level of the anterior end of the cerebral organs (Fig. 8g).

The cerebral organs, 510  $\mu\text{m}$  long, are very large and extend behind the cerebral ganglia (Fig. 6c). For about 180  $\mu\text{m}$  of its length, each is closely adjacent to the brain, which has a length of 460  $\mu\text{m}$ . Anteriorly, the organ is circular in transverse section, but it becomes oval farther posteriorly (Fig. 7g), and its posterior glandular portion is circular (Fig. 9b). The cerebral organ canal, ciliated and 220  $\mu\text{m}$  long, begins at one of the secondary grooves of the anterior oblique cephalic grooves on the midlateral portion of the head, and is directed posteromedially. It widens just before entering the cerebral organ and forms a U-shaped, ciliated sensory portion (Fig. 8h). The epithelium of this is 20  $\mu\text{m}$  thick. The canal has a widened lateral portion with a dorsally directed small groove lined with unciliated epithelium 8  $\mu\text{m}$  thick (Fig. 8h). Farther posteriorly, the canal divides into a narrow sensory canal and a short, sac-like canal that has a T-shaped configuration when seen in transverse sections (Fig. 8a), and the dorsally directed groove disappears (Fig. 8a, b).

The sensory canal, 20  $\mu\text{m}$  thick, lies on the side closest to the brain (Figs. 7g, 8a, b). It consists of a ciliated wall in which the sensory cells containing eosinophilous cytoplasm are arranged in a row. Farther posteriorly, the ciliation disappears and the canal enters a mass of eosinophilous glands about 40  $\mu\text{m}$  long and 20  $\mu\text{m}$  wide (Figs. 6c, 9a, b). The total length of the canal is about 260  $\mu\text{m}$ .

The anterior portion of the sac-like canal (Fig. 6c), 80  $\mu\text{m}$  by 60  $\mu\text{m}$  in diameter and about 110  $\mu\text{m}$  long, has a wall 10  $\mu\text{m}$  thick. Its unciliated epithelium consists of slightly eosinophilic cells 6  $\mu\text{m}$  wide; these are arranged in one or two layers (Fig. 8b). Its

Table 1.—Summary of the main morphological characters of eleven marine nemerteans related to the genus *Nipponnemertes* including *N. fernaldi*, new species.

Character	Character states	Coding
1. Body color	With pattern	0
	Without pattern	1
2. Cephalic grooves	Two pairs of oblique cephalic grooves and dorsomedial longitudinal grooves	0
	Two pairs of fluted cephalic grooves and inconspicuous oblique grooves	1
	A pair of shallow oblique fluted grooves	2
	A pair of lateral transverse grooves	3
	No record	4
3. Cephalic grooves	Anterior oblique cephalic groove subdivided by 14 secondary grooves, ventrolateral surface of head with 7 secondary grooves, posterior oblique cephalic grooves originating at the end of dorsomedial longitudinal grooves, and dorsomedial longitudinal grooves forming anteriorly a pair of epidermal folds	0
	No record	1
4. Ocelli	Numerous large ocelli in four groups	0
	In lateral rows	1
5. Body wall	Longitudinal muscle layer well developed	0
	No record	1
6. Diagonal muscles	Present between circular and longitudinal muscle layers	0
	No record	1
7. Dermis	Thick	0
	No record	1
8. Rhynchocoel	Nearly equal to body length	0
	No record	1
9. Proboscis sheath	Composed of interwoven circular and longitudinal muscles	0
	No record	1
10. Rhynchodeum	Provided with a circular muscle layer	0
	No record	1
11. Precerebral septum	Composed of muscular septum surrounding rhynchodeum	0
	Composed of muscular bundle	1
	No record	2
12. Proboscis diaphragm	Provided with central stylet-basis complex	0
	Provided with a single central stylet and a barrel-, bell-, drop-shaped or conical basis	1
	No record	2
13. Basis of central armature	With posteriorly-inserted accessory stylet	0
	No record	1
14. Stylet bulb	With a plate-like muscular wall and a thick layer of glandular cells	0
	No record	1
15. Accessory stylet pouches	2	0
	2 or more	1
	No record	2
16. Proboscis nerves	11	0
	12–14	1
	14	2
	14–16	3
	15	4
	20	5
17. Mouth	No record	6
	Opening into rhynchodeum	0
18. Esophagus	Anterior to brain surrounded by longitudinal muscle	0
	No record	1
19. Foregut caecum	Esophageal caecum present	0
	Stomach caecum present	1
	No record	2

Table 1.—Continued.

Character	Character states	Coding
20. Intestinal caecum	Without anterior diverticula but with lateral ones	0
	With a pair of anterior diverticula sending off numerous branches	1
	No record	2
21. Intestinal caecum and diverticula	Intestinal caecum with anterior branches or pouches and two pairs of lateral diverticula, and intestinal diverticula branched	0
	No record	1
22. Blood vascular system	With three longitudinal vessels, middorsal vessel with single vascular plug	0
	No record	1
23. Nervous system	Brain and lateral nerves covered by a thin neurilemma and a thick layer of fibrous connective tissue, nervous system without neurochord cells, and accessory lateral nerves, middorsal nerve extending anteriorly beyond brain, and lateral nerve cords with myofibrillae and peripheral nerves	0
	No record	1
24. Ventral ganglia	Not distinctly separated from dorsal ganglia	0
	Posteriorly separated	1
	No record	2
25. Dorsal ganglia	Without bifurcated fiber core	0
	No record	1
26. Nerve cords	Paired midgut, foregut, and esophagus nerves originating from ventral brain	0
	No record	1
27. Frontal organ	Present	0
	No record	1
28. Cephalic glands	Well developed and reaching posteriorly to cerebral ganglia	0
	Prominent but reaching posteriorly to cerebral ganglia	1
	Moderately developed	2
	Small	3
29. Submuscular glands	Abundant in brain region	0
	Limited to a narrow area	1
	Absent	2
	No record	3
30. Cerebral sensory organ	Large and extending behind cerebral ganglia	0
31. Cerebral sensory organ	With neurilemma and cerebral organ canal branching into medial sensory canal and lateral sac-like canal with two kinds of glandular masses	0
	No record	1
32. Cerebral organ canal	Open laterally in front of brain	0
	Far anterior to brain	1
	No record	2
33. Excretory system	Pair of excretory pores lateral to nerve cords and situated in posterior portion of nephridial region	0
	Situated at middle of nephridial region	1
	Situated behind cerebral sensory organs	2
	No record	3
34. Sexes	Separated	0
	No record	1

very first part is still T-shaped in transverse section, and still has a shallow, dorsally directed lateral groove (Fig. 8a). The sac-like canal is succeeded by a narrow duct, 180  $\mu\text{m}$  long, surrounded by cyanophilous

glands about 20  $\mu\text{m}$  long and 15  $\mu\text{m}$  wide (Figs. 6c, 7g, 9a).

The internal configuration of the sensory canal and the sac-like canal can be understood by studying transverse sections at

their proper levels in Figures 6c, 7g, 8a, b, 9a, b. The term "sac-like canal" is used here because this structure has a thick epithelium and also because it has cyanophilous glands (cf. Crandall 1993a).

The ganglionic mass of the cerebral organ is mostly confined to the anterior portion of the organ, where it surrounds the sensory canal and sac-like canal. Glands are not present at the bifurcation of the cerebral organ canal (Fig. 8h). All of the organs are covered with connective tissue from the neurilemma of the cerebral nerve. The thick nerve from the posterior end of the dorsal ganglion enters the posterior portion of the glandular mass of the sac-like canal (Figs. 6c, 7g).

*Excretory and reproductive systems.*—The excretory tubules wind around and along the lateral blood vessels (Figs. 4a, 7c, d, f). In the holotype, they extend from the level of the posterior portions of the cerebral sensory organs to the level of the posterior part of the pylorus; the region they occupy is 3.6 mm long. The efferent duct, beginning in the middle portion of the nephridial region, is conspicuous and extends above and lateral to the lateral nerve cord, reaching the excretory pore on the lateroventral side of the body. The pore is ventral to the lateral nerve cord, and is at the level of the mid-pyloric region. The efferent duct of the left side, about 120  $\mu\text{m}$  long, is much longer than that of the right side. The left excretory pore is located about 810  $\mu\text{m}$  farther posterior than the right pore.

In paratype 1, the excretory tubules extend from the level of the posterior end of the cerebral sensory organs to a short distance behind the pylorus; the region they occupy is 5.4 mm long. The efferent ducts, beginning in the posterior portion of the nephridial region, are 200  $\mu\text{m}$  long; the excretory pores are situated at their anterior ends.

The ovaries of the fully mature holotype specimen are located near the beginning of the intestinal caecum, and are arranged irregularly between the intestinal diverticula

(Figs. 2f, 4a, b). Gonoducts open at gonopores on the lateral sides of the body. In the other two sectioned paratypes, both males, the gonads are undifferentiated and lack gonoducts.

*Swimming.*—The specimens were observed to swim vigorously in the laboratory when the container was shaken. During swimming the body became more flattened and the swimming pattern was anguilliform, resembling that of a *Cerebratulus*. Swimming has been described for the hoplonemertean *Nipponnemertes punctatulus* (Coe 1905) and *N. pulcher* (McIntosh 1873, Brunberg 1964, Berg 1972).

#### Discussion of Systematics\*

The species described here is a member of the suborder Monostilifera (sensu Gibson 1995), owing to the morphology of the armature of the proboscis and the location of the mouth opening. It fits in the family Cratenemertidae (Friedrich, 1968) with respect to the following characteristics: rhynchoel wall with interwoven muscle layers of the proboscidial sheath; rhynchoel extending nearly to the posterior tip of the body; cerebral organs large, extending behind the cerebral ganglia (Berg 1985, Gibson & Crandall 1989, Crandall & Gibson 1998).

The cratenemertid genus *Nipponnemertes* (type species: *Nipponnemertes punctatulus* (Coe, 1905), recently designated by Crandall (2001), is closest to the present species, especially with regard to the features cited in the generic diagnosis. Comparisons with other related species are found in Tables 1 and 2.

The arrangement of ocelli in *N. fernaldi* is virtually the same as that of all other Pacific *Nipponnemertes*, and the close juxtaposition of the end of the rhynchoel and the two posterior anastomoses also occurs in a few species of *Nipponnemertes*. In most cratenemertids, the anastomoses of blood vessels and lateral nerves are decid-

Table 2.—Character matrix for species of *Nipponnemertes*. Character numbers refer to Table 1.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34		
<i>N. drepanophoroides</i>	0	4	1	1	1	1	1	1	0	1	2	2	1	1	2	6	0	1	2	2	1	1	1	1	2	1	1	1	0	1	0	3	1			
<i>N. pacificus</i>	0	3	1	1	1	1	1	0	0	2	2	1	1	1	0	2	0	1	2	0	1	0	1	2	2	1	1	1	1	0	1	0	2	0		
<i>N. occidentalis</i>	1	3	1	1	1	1	0	1	0	2	2	2	1	1	0	6	0	1	0+1	1	1	1	1	2	1	1	1	1	2	0	1	2	0	0		
<i>N. punctatulus</i>	1	2	1	0	0	1	0	0	0	2	2	1	1	1	0	1	0	1	2	0	1	0	1	0	0	0	1	1	0	1	0	0	0	0	0	
<i>N. bimaculatus</i>	0	1	1	0	0	1	0	0	0	2	2	1	1	1	1	3	0	1	0	0	1	1	1	0	0	0	1	1	2	1	0	0	0	2	0	
<i>N. pulcher</i>	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	1	0	1	2	0	1	0	1	0	0	0	1	0	0	0	1	0	2	0	0	
<i>N. africanus</i>	1	4	1	1	1	1	0	0	1	2	2	2	1	1	0	0	1	2	2	2	1	1	1	2	1	1	1	0	1	3	0	1	0	2	0	0
<i>N. magnus</i>	0	4	1	1	0	1	0	0	1	2	2	2	1	1	2	5	0	1	2	2	1	1	1	2	1	1	1	1	3	3	0	1	0	1	0	0
<i>N. marioni</i>	0	4	1	0	0	1	0	0	1	2	2	2	1	1	0	4	0	1	2	0	1	1	1	2	1	1	1	0	0	3	0	1	1	0	0	0
<i>N. schollaerti</i>	0	3	1	1	0	1	0	0	1	2	2	2	1	1	0	2	0	1	2	0	1	1	1	2	1	1	1	0	0	0	1	0	0	0	0	0
<i>N. fernaldi</i>	0	2	0	0	0	0	0	0	0	0+1	0	0	1	0	1	2	0	0	2	0	0	0	0	0+1	0	0	0	2	1	0	0	0	0	0	0	0

edly posterior to the end of the rhyncho-coel.

Concerning the structure of the cerebral organs, Gibson (1988) stated that the cerebral organs of Antarctic species of *Nipponnemertes* resemble those of inaequifurcate Eurentantia in being large and elaborate structures, close to and reaching behind the cerebral ganglia; furthermore, their cerebral canals are divided. Gibson (1988) also pointed out that the cerebral organs of *Nipponnemertes* appear much more highly evolved than those of almost all Monostilifera, and that their organization and position may be indicative of a closer evolutionary relationship to Reptantia than has previously been appreciated. On the basis of these features, Gibson (1988) pointed out that there are similarities between *Nipponnemertes* and Reptantia (Inaequifurcata). Crandall (1993a) wrote that *N. bimaculatus* (*Amphiporus bimaculatus*), now known to be a cratenemertid, possesses a canal that divides, just after entering the cerebral organ, into two branches: a sensory branch having a uniform elliptical cross-section throughout its length, and a shorter branch of similar size but complex shape, lined with characteristic ‘sac-like’ epithelium.

*Nipponnemertes bimaculatus* from Rishiri Island in Hokkaido, Japan (Iwata 1954) has large cerebral organs situated at the lateral side of the brain and extending posteriorly behind the brain. In addition, the muscle layer of the proboscis sheath is interwoven, a feature clearly evident in my slides. The cerebral organs are like those in the present species (Fig. 9c, d). *Nipponnemertes punctatulus* from Onomichi (Iwata 1951) has several characters of the genus: large cerebral organs situated at the lateral side of the brain and extending posteriorly behind the brain; the interwoven muscle layer of the proboscis sheath; similarity of the cerebral organs to those of *N. bimaculatus* (Fig. 9e, f); and a distinct rectum with circular muscle sphincter.

*Nipponnemertes fernaldi* is distinctive because of the following features: a central

stylet-basis complex of unique structure; a bulblike stylet bulb with a platelike muscular wall and a thick layer of glandular cells; an intestinal caecum with four branches or pouches and two pairs of lateral diverticula; a pair of dorsomedial longitudinal epidermal folds in the anterior region. These features have not been reported for cratenemertids of the genus *Nipponnemertes* until now. The combination of characters found in *N. fernaldi* decidedly excludes it from the existing species of *Nipponnemertes* (Griffin 1898, Coe 1901, 1905; Punnett 1903, Wheeler 1934, 1940; Iwata 1951, 1954; Friedrich 1968, Berg 1972, 1985; Gibson 1995, Crandall & Gibson 1998). Because of this, a new species is proposed to accommodate it.

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\* Editor's note: The author mentioned the taxon as *Nipponnemertes fernaldi* nov. sp. in an abstract published in the Japanese journal *Taxa* (no. 11, 2001) in September 2001. However, this publication of it did not make the name 'available', since no type specimen was designated therein as required by Article 72.3 of the International Code of Zoological Nomenclature (4th Ed., 1999). The full description and designation of type specimens in this issue of the *Proceedings of the Biological Society of Washington* 114(4):833–857, make the name available for the first time, and it is correctly used therein as *Nipponnemertes fernaldi* n. sp.